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OBSERVATIONS ON THE COURTSHIP BEHAVIOR OF *AMBYSTOMA JEFFERSONIANUM*

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The evolution of courtship behavior has recently been shown to have phylogenetic significance (Noble, 1931). The essential similarity of the stages of this activity among related species has been found to occur among salamandrids and was demonstrated among plethodontids by Noble and Brady (1930). Although the same condition appears to hold true among the ambystomids as well, notes already published on the courtship of *Ambystoma jeffersonianum* indicate some deviation from the general pattern of this group (Mohr, 1931). It was therefore considered important to secure, if possible, the complete courtship story of this species. Mohr (1931) has described the essential points of the "Liebesspiel" but has given no detailed account of the activities of mating individuals and has not reported any instances of the actual picking up of the spermatophore by the stimulated female. This paper will present the complete sequence of events from the inception of courtship to the acceptance of the spermatophore.

The individuals under observation were collected on the nights of March 31 and April 10 in the vicinity of Montauk, Long Island, near a large shallow pond about one foot in its deepest section. The salamanders were found on land, under sticks, stones, and mosses. No eggs were seen in the field and apparently no individuals had entered the water at that time.

The activities of two adult males and three noticeably gravid females were recorded the greater part of April 1. On April 4, each of the males of this group received two anterior lobes of fresh pituitary from *Rana pipiens* individuals. Courtship occurred again the night of April 5, and during April 6. A second group of the same number of males and females was observed continuously over a period of five hours on April 11. Between the times of study the sexes were separated and kept in the laboratory icebox.

Observations were made in a dark room illuminated by three red lights of 10-watt power each, although an ordinary electric light was

found to have little effect upon the progress of activities. An Alberene tank (60×30×30 cm.) half filled with tap water was used. The temperature varied between 50° and 55° F. In three of the four periods of study the "Liebesspiel" began in less than fifteen minutes after the introduction of the salamanders into the aquarium and at least sixty spermatophores were deposited by the four males during the entire study.

The initial records made at the time of observation graphically present the outstanding features of the story:

At 10:06 A.M.—A male is going through a series of rapid vibratory movements of his body accompanied by vigorous waving of his tail from side to side. This continues for two minutes.

10:07 A.M.—The other male climbs astride a female and embraces her with his forelimbs just behind her head. After two minutes in this position he clasps her around her hind legs with his head over her tail. He leaves her after a minute and stalks ahead but returns immediately to embrace her again, this time behind the forelegs. Together they swim almost around the tank, the male's body undulating all the time. For thirty seconds they settle quietly in a corner and then make a complete trip around the aquarium. Another few seconds of inactivity after which the male leaves the female's back and proceeds ahead of her. His whole body is undulating and his tail is raised and waving. At the same time he appears to be rubbing his cloacal region over the bottom of the tank. This movement ceases while he pursues another

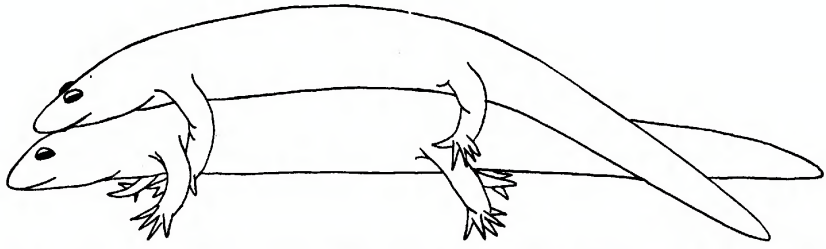

Fig. 1. First position of male in embrace. Male clasping female just behind forelimbs with tip of his snout between anterior corners of her eyes.

female for a few seconds. However, he returns to the first female whom he embraces again at 10:11. They swim around the tank and settle quietly. At 10:13 he departs and moves slightly ahead with wriggling body and rapidly waving tail. First, his head is raised and then his tail until it is at a 90° angle with the bottom of the tank. The female's snout is closely applied to the male's cloaca. In two minutes he deposits two spermatophores about 2.5 cm. apart. The female fails to secure either or even display any interest in them. The male returns to clasp her again for thirty seconds and then leaves to repeat the same wriggling, vibratory movements of his body. As before, the female's snout is near his cloaca as he deposits a third spermatophore and almost immediately a fourth. The female picks up neither. The male starts after another female.

An analysis of all the data acquired confirms the above account and shows that the "Liebesspiel" is begun when a male climbs astride a female and embraces her. If he happens to crawl over her in such a fashion that his head rests over her cloaca he immediately turns directly about and encircles her body with his forelimbs either just before or behind her forelegs. (See Fig. 1.) Both positions have been observed over and over again although the latter is the more common. In a few instances one leg has been seen placed before and one behind her forelegs. The male's forefeet are usually pressed with the inner surface flat against the female's body with digits of the opposite forefeet just touching or alternating. When the female attempts to dislodge the male the digits of the forelimbs are interlocked so that they stand away from her body or the forefeet are placed one over the other. The amount of strength needed to maintain the embrace apparently determines the type of hold used by the male (Fig. 2). It has been noticed several times that a male may also clasp the female slightly with his hind legs when other individuals threaten to break his hold.

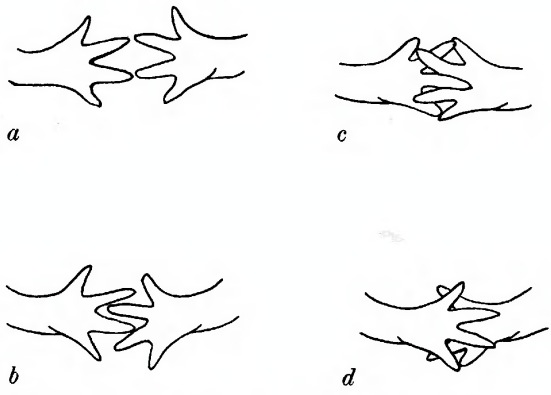

Fig. 2. Diagrams of positions of male's forefeet in embrace.
a. Digits touching.
b. Digits alternating.
c. Digits interlocked.
d. One foot over the other.

Once the male has established his clasp on the female a variety of events may occur and the embrace may terminate in a few seconds or continue for minutes. Unless the male is sufficiently stimulated to proceed rapidly to the deposition of the spermatophore and the preceding activities there is usually an extended period of interesting "play" when the pair alternately swim about or remain quiescent. Both in-

dividuals have been seen to be active at the same time with their bodies lashing back and forth. Sometimes only the female shows any inclination to move about and she will swim around with the inactive male on her back. The male's efforts are more effective, often lifting the pair to the surface as his body lashes vigorously from side to side. At this point his chin is rubbed persistently over the female's head. Usually the tip of the male's snout is not thrust farther forward than the anterior corners of the female's eyes. However, as the "Liebesspiel" progresses a courting pair is observed to settle quietly and the male gradually works his body forward until his chin is applied to her snout (Fig. 3), and he rubs her excitedly. Sometimes his hind feet appear to stroke her body too. A typical notation gives an accurate idea of this phase:

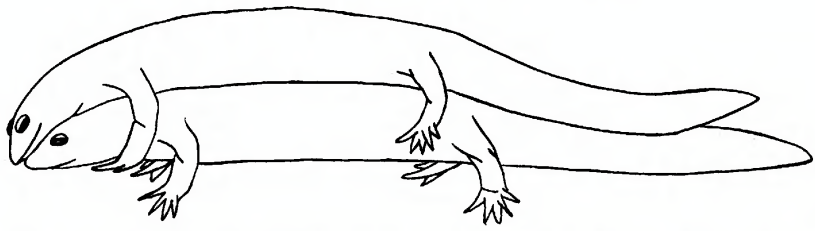

Fig. 3. Second position of male in embrace. Head in position for rubbing female's snout with his chin.

10:10 A.M.—Male embracing female and as he moves forward to rub her snout he slackens his grasp considerably, but when she makes a move as if to escape he tightens it at once.

This stage is usually terminated quickly and the male releases his hold to move forward and ahead of the female. As he proceeds his whole body is tremulous and his tail undulates unceasingly. The vibrating of his body continues and a sort of tenseness appears as his feet are lifted from the bottom and held rigidly outstretched. At the same time his waving tail assumes a position at right angles to his body. Only the tip of his snout and cloaca are in contact with the surface of the aquarium and as the quivering continues he deposits a spermatophore. In the majority of cases a male has been seen to produce two or three spermatophores within a minute or two, about 1.5 cm. apart. It should be noted at this point that the extrusion of spermatophores has seldom been observed when no female is at hand and often the male curtails the process when the female shows indifference or half-hearted interest. In the latter case the male ordinarily returns to embrace her and repeat the rubbing of her snout with his chin.

When the female has been sufficiently stimulated she approaches and attempts to bring her snout to the male's cloaca. This usually results in the male's depositing one or generally several spermatophores. She moves forward with the male as he continues to produce them. Consequently, first her chin and then her body pass over the spermatophore, and if she is undisturbed her cloaca finally settles down upon it. Unfortunately the interference of other individuals or the return of the courting male often ends the story at this point. However, two cases of removal of the spermatophore head were carefully noted. One record is as follows:

10:43 A.M.—Female's cloaca directly over the spermatophore and she rests there with only slight movement of her body. Other individuals approaching move her but not before a considerable portion of the spermatophore head has entered her cloaca.

The one instance of complete engulfment of the spermatophore is recorded as follows:

Male deposits one spermatophore and then a second about 2 cms. before it. Female follows him, nose at his cloaca. Passes her body over first spermatophore and settles cloaca over it. Her body shows slight undulations in pelvic region. Spermatophore picked up in about one minute.

The exact mechanism of the introduction of the spermatophore into the female's cloaca is not definitely determined, but as in *A. maculatum* the cloacal lips appear to be the chief means. Certainly the hind limbs are not used as described by Gasco (1881) for the female axolotl.

The recognition of the female by the male appears to be easily accomplished. Whether it is a matter of attraction effected by odor or an optical or tactile stimulus induced by the size of the gravid individual remains undetermined. Unlike *A. opacum* (Noble and Brady, 1932) the males of *A. jeffersonianum* evince sustained interest only in the opposite sex and the rapidity with which they can determine the head end of the females is very striking. In only a few instances of the great number of embraces that were watched did the male clasp the posterior portion of the female's body and continue to hold her in that manner. Two cases of genuine interest of one male in another were carefully noticed and recorded because, as mentioned above, members of the same sex usually remained indifferent to each other unless a female was involved and both males were striving to dislodge each other and court the female without interference. An embrace of males for a period of one and a half minutes is described in the records.

10:47 A.M.—Two males are nosing each other and one clasps the other around his hind limbs. 10:48—Both clasping. They curl into a wriggling mass, nosing cloacæ.

10:48½—One still holding the other who breaks loose by frantically lashing his body.

A somewhat more interesting observation was made later the same day.

11:18 A.M.—One male attempting to embrace another whom he is holding just before his hind legs. The clasping male is momentarily shaken off but renews his hold now behind the forelimbs. His forefeet are pressed against the protesting individual's body and the digits are clearly interlocked. The salamander being held squirms and writhes and tries to pry off his captor by pushing with his hind feet. This protest continues until he breaks loose at 11:22 A.M.

This record is followed by the note that at

11:23 A.M.—The situation is reversed and the captor now becomes the captive and the activity is again vigorous until 11:24 when a female swims by and the males still in embrace clasp her too.

Possibly the relatively passive reaction of the female to embrace as contrasted with the male's violent avoiding reaction to the same situation serves to guide the courting male to the right sex. However, this cannot be the whole story, for females undesirous of attention were seen to attempt actively to dislodge the unwelcome males who continued to cling tenaciously. Further study along experimental lines will be necessary to clear up this point.

CONCLUSIONS

1.—The courtship of *A. jeffersonianum* as described by Mohr (1931) is confirmed and further details observed.

2.—The male embraces the female from above either before or behind the forelimbs.

3.—The male stimulates the female to sexual activity by undulations of his body and by vigorous rubbing of his chin first over her head and then her snout.

4.—The male when extruding a spermatophore has his feet outstretched and tail raised. His entire body undulates. The female is further stimulated by close application of her snout to his cloaca at the time of deposition.

5.—The female secures the spermatophore with her cloacal lips. She may receive the whole spermatophore but more often removes only the head.

6.—Courting males of *A. jeffersonianum* remain almost completely indifferent to each other except in the presence of a female whom both attempt to embrace.

7.—Two cases of one male embracing another male for a prolonged period are reported.

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